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PHYLOGENY OF THE TROIDINE BUTTERFLIES (LEPIDOPTERA: PAPILIONIDAE) REVISITED: ARE THE RED-BODIED SWALLOWTAILS MONOPHYLETIC?

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Abstract

The phylogenetic relationships and biogeography of troidine butterflies are reassessed. The subtribe Troidina is considered to comprise the following generic groups, representing vicariant separation within western, central and eastern Gondwana respectively: *Parides* Hübner + *Euryades* C. & R. Felder; the 'red-bodied swallowtails' *Atrophaneura* Reakirt + (*Pachliopta* Reakirt + (*Losaria* Moore, stat. rev. + *Cressida* Swainson)); and the 'birdwings' *Trogonoptera* Rippon + (*Troides* Hübner + *Ornithoptera* Boisduval). *Pharmacophagus* Haase, with its sole species *P. antenor* (Drury) from Madagascar, is retained as a subgenus of *Pachliopta*. The suggestion that *Pharmacophagus*, *Cressida* and *Euryades* are relict taxa is rejected.

Introduction

Recent studies on the phylogeny and biogeography of troidine butterflies have shown little agreement. For example, Hancock (1983, 1988), Miller (1987) and Parsons (1996a, b) produced classifications which differed markedly, particularly with regard to the placement of *Atrophaneura* Reakirt and its allies. Until now, it has not been possible to reconcile these differences. However, a recent study by Braby *et al.* (2005) has strongly suggested that almost all previous phylogenies were based on a misconception - that *Cressida* Swainson and *Euryades* C. & R. Felder were sister genera. The suggestion by Braby *et al.* (2005) that this is not the case enables several morphological characters, previously considered to be homoplasious (*e.g.* the distinctive red abdomen seen in several genera, including *Cressida*), to be reassessed and seen as potential synapomorphies.

Morphological relationships

Monophyly of the tribe Troidini and subtribes Battina and Troidina has been recognised by most recent authors (*e.g.* Hancock 1983, Miller 1987, Braby *et al.* 2005) and appears well established. Subtribe Battina contains the sole genus *Battus* Scopoli, known only from North and South America. It is of either North American (Hancock 1983) or Gondwanan (Braby *et al.* 2005) origin. Subtribe Troidina contains all the remaining genera in the tribe and is of undoubted Gondwanan origin. Three distinct groups of genera are recognisable on morphological grounds; these appear to be vicariant groups originating in eastern, western and central Gondwana respectively. Genera in this subtribe are united by numerous characters (Hancock 1983, Miller 1987), including the presence of a basal seta on the subdorsal tubercles of the first instar larva (Igarashi 1984) and red hairs on the head and thorax (and often the abdomen) of the adult, a condition not seen elsewhere in the Papilionidae. Larval food plants for the Troidini are all members of the family Aristolochiaceae (*Aristolochia*, *Pararistolochia*, *Thottea* and *Apama*).

***Trogonoptera* Rippon, *Troides* Hübner and *Ornithoptera* Boisduval**

Although disputed by Parsons (1996a, b), monophyly of this group of genera, the 'birdwings', is well established. The relationship *Trogonoptera* + (*Troides* + *Ornithoptera*) was suggested by Hancock (1983, 1991) and supported by Miller (1987, as subordinate groups within *Troides*), Hancock and Orr (1997) and Braby *et al.* (2005). [Note that in Fig. 3 of Braby *et al.* (2005), the names *Troides* and *Troides* (*Ornithoptera*) should be transposed]. The genera are restricted to the Indo-Australian region. They share the following characters: abdomen without red hairs; juxta U-shaped; pseuduncus generally long, apically pointed and with a basal suture (secondarily reduced in *Trogonoptera*); aedeagus short; bursa large with membranous ductus bursae and well developed appendix bursae; signum comprised of concentric folds (all characters similar to those seen in *Battus*). Defining characters were noted by Hancock (1983) and Miller (1987).

***Parides* Hübner and *Euryades* C. & R. Felder**

Although their evidence was not well supported, Braby *et al.* (2005) suggested that these two genera were sister groups. Significantly, they found no evidence of a relationship between *Euryades* and *Cressida*. The genera occur in Central and/or South America and share the following characters: abdomen with red hairs, especially posteroventrally; juxta Y-shaped with narrow anterolateral expansions; pseuduncus long, apically pointed and with a basal suture; aedeagus short; female bursa with membranous ductus bursae and no appendix bursae. Larvae with spinose setae on subdorsal tubercles retained beyond the first instar [absent in other groups and *Battus*] (Parsons 1996a). In *Parides* the valvae are entire, the aedeagus broad, the bursa large and the signum broadly C-shaped and transverse. In *Euryades* the valvae are reduced, the aedeagus narrow, the juxta with long apodemes, the ovipositor lobes melanised, the bursa small and the signum absent.

***Atrophaneura* Reakirt and allies**

Monophyly of this group has not been recognised previously. Four Indo-Australian genera and one Madagascan subgenus are included. All have extensive red hairs and scales on the abdomen, much better developed than in *Parides* and *Euryades*. The female bursa has no appendix bursae and the signum, when present, is neither broadly C-shaped nor formed of concentric folds. The first instar larva has the sclerotised, setose apex of the tubercles rounded and dome-like [pinnacle or pagoda-like in other groups] and the pupa has the head short and truncate in lateral view [distinctly produced anterolaterally in other groups and *Battus*] (Igarashi 1984, Parsons 1996a).

Atrophaneura

This is an eastern and southeast Asian genus of some 27 species referred to the *latreillei* and *nox* groups by Hancock (1980, 1988). Miller (1987) regarded these two groups as subgenera included in an unresolved trichotomy with *Parides*. It differs from other genera in the group by the retention of a well developed scent organ on the male hind wing, a distinct, apically pointed pseuduncus with a basal suture, a short, broad aedeagus, and a large bursa with membranous ductus bursae. The juxta appears to be a modification of the Y-shape, while the signum is longitudinal, expanded anteriorly and narrowly tapered posteriorly. On the hind wing the tail is broadly spatulate (*latreillei* group) or absent (*nox* group) and white areas, when present, at most weakly enter the discal cell. The valvae are entire or weakly emarginate. Larva with a distinct supraspiracular tubercle on first abdominal segment and pupa with distinct, apically pointed subdorsal projections on abdominal segments 2-10 and a broad lateral flange on segment 4 (Igarashi 1984).

Losaria Moore, *Cressida* Swainson and *Pachliopta* Reakirt
These genera differ from *Atrophaneura* in the reduction of the scent organ and shortened vein 1A+2A on the hind wing, elongate and narrow aedeagus, and sclerotised posterior part of the ductus bursae [not evident in *Cressida*]. They occur primarily in the Indo-Australian region, with a single species in Madagascar. The tegumen and socii are frequently enlarged and the valvae are usually reduced. Larva with supraspiracular tubercle on first abdominal segment usually absent and pupa with apically rounded or truncate subdorsal projections on abdominal segments 4-7 (and very weakly on segment 8) and with lateral flange on segment 4 present or absent.

Losaria
This is a Southeast Asian genus of four species referred to the *coon* group by Hancock (1983, 1988). An affinity with *Pachliopta* was recognised by Igarashi (1984), Hancock (1988) and Miller (1987), who placed it either as a subgenus of the latter (Miller 1987) or as a synonym of it. Because of its apparent sister-group relationship with *Cressida*, it is here raised to generic status (stat. rev.), characterised by the elongate forewing discal cell, deeply indented margin to cell Cu of the male hind wing, strongly petiolate and club-shaped tail, posteriorly downcurved abdomen, Y-shaped juxta with broad anterolateral expansions, often reduced but apically acute pseuduncus with a basal suture, reduced valvae, and large bursa with a small, round signum. A sphragis is present in one species and in two the 'red' abdominal markings are yellow. When the hind wing has a white area that crosses the discal cell, the apex of the cell is black. Larva with supraspiracular tubercle on first abdominal segment absent (Igarashi 1984) and subdorsal tubercles on abdominal segments 2 and 3 conspicuously reduced (Weintraub 1995). Pupa with subdorsal projections large and lateral flange present (Igarashi 1984).

Cressida
This is a monotypic Australian genus previously placed with *Euryades*. It differs from related genera in the absence of a tail, large precostal hindwing cell, vestigial bursa and lack of a signum. It shares with *Losaria* the elongate forewing discal cell, deeply indented margin to cell Cu of the male hind

wing, black apex of the hindwing discal cell, posteriorly downcurved abdomen, presence of a Y-shaped juxta with broad anterolateral expansions, apically pointed pseuduncus with a basal suture, and similarly reduced valvae. With both *Euryades* and *L. palu* (Martin) it shares a well-developed sphragis but these appear to be independently acquired and not homologous (Orr 1988, 1995). Larva with supraspiracular tubercle on first abdominal segment absent and all other tubercles reduced; pupa with head truncated in lateral view, subdorsal projections small and lateral flange absent (Igarashi 1984). The male valvae also resemble those of *Euryades* but other characters of *Euryades* [including the socii, pinnacle-like apex of the first instar larval tubercles and anterior projection of the pupal head in lateral view (Miller 1987, Parsons 1996a)] more closely resemble those of *Parides* than those of *Cressida*. The distinctively red abdomen, dome-like apex of the first instar larval tubercles and truncated pupa in *Cressida* provide the best evidence of the affinity of this genus with others in the *Atrophaneura* complex.

Pachliopta

This genus contains 13 species in the Indo-Australian region and one in Madagascar. They were referred to the *polydorus*, *hector* and *antenor* groups by Hancock (1988). The genus is characterised by the spatulate tail [reduced in *P. polydorus* (Linnaeus)], T-shaped juxta, short, blunt pseuduncus with basal suture absent (at least medially), valvae either entire or vestigial, and large bursa with an elongate signum of uniform width. When the hind wing has a white area that crosses the discal cell, the apex of the cell is also white. Larva with subdorsal tubercles not conspicuously reduced. Two subgenera are recognised: *Pachliopta* Reakirt and *Pharmacophagus* Haase. In both the pupa is strongly S-shaped in lateral view and has the lateral flange on abdominal segment 4 present; the anal segments and cremaster, viewed ventrally, are also very similar (Igarashi 1984, Parsons 1996c).

Subgenus *Pachliopta*

This subgenus contains all the Indo-Australian species. Braby *et al.* (2005) noted that *P. hector* (Linnaeus) was more closely related to species in the *polydorus* group than to *P. antenor*, with which it was associated by Hancock (1988). This is supported by the wide separation between tergite 8 and the hypertrophied tegumen and socii, and by the vestigial valvae (see Miller 1987); thus *P. hector* is here subsumed into the *polydorus* group. Larva with the supraspiracular tubercle on the first abdominal segment reduced to a spot in *P. hector* (Woodhouse and Henry 1942), absent in other species (Woodhouse and Henry 1942, Igarashi 1984). Pupa with subdorsal projections large and lateral flange well developed (Igarashi 1984).

Subgenus *Pharmacophagus*

The sole species [*P. antenor* (Drury)] occurs in Madagascar. It differs from subgenus *Pachliopta* in the presence of normal (not vestigial) valvae, a well developed supraspiracular tubercle on the first abdominal segment and reduced subdorsal tubercles on abdominal segments 3 and 4 of the larva, and small subdorsal projections and lateral flange on the pupa (Parsons 1996a, c). The tail is relatively narrow, similar to that of *P. hector*. Often regarded as a distinct genus, the form of the juxta, pseuduncus and signum, and the presence of blue-green hindwing scales in a rare form of *P. hector* (Woodhouse and Henry 1942), support a close relationship with *Pachliopta*. It was regarded as a subgenus of the latter by Hancock (1993).

Discussion

Pharmacophagus was regarded as a distinct genus by Igarashi (1984), Miller (1987), Parsons (1996a, b, c) and Braby *et al.* (2005). Igarashi (1984) considered it to be 'closely related to *Pachliopta* but highly specialised'. Miller (1987) placed it at the base of the subtribe, *i.e.* as the most primitive genus. However, he identified only one character that unambiguously separated it from *Pachliopta* - the 3-segmented palpi with a 'basal fleck' present. All other genera in the Troidina have 2-segmented palpi [which appear to have formed by fusion of segments 1 and 2: see illustrations in Miller 1987] and no 'basal fleck'. Hancock (1989) suggested that the 3-segmented palpi of *P. antenor* resulted from a secondary loss of this fusion (character reversal) and that the 'basal fleck' was also secondarily acquired, with neither homologous to the condition seen in *Battus*. Its placement as sister genus to *Ornithoptera* (Parsons 1996a, b) was disputed by both Hancock and Orr (1997) and Braby *et al.* (2005) and is not sustainable.

In their molecular study, Braby *et al.* (2005) also regarded *Pharmacophagus* as basal to all other genera in the subtribe. However, only one of the three genes studied (*EF-1α*) supported that arrangement. The *ND5* gene produced a trichotomy of (i) *Pharmacophagus*, (ii) *Cressida*, and (iii) all other genera, whereas the *COI-COII* gene produced an unresolved polytomy of all genera plus *Battus*. Their combined analysis also produced a clade with *Pharmacophagus* at its base, but the placement of *Papilio* Linnaeus as sister to the Parnassiinae in the combined clade, and the placement of the Baroniinae and Parnassiinae between *Graphium* Scopoli and the Troidini (or *Papilio* + Troidini) in all of them, suggest that the use of these genes in resolving higher-level groupings requires considerable caution. Unreliability of the *ND5* gene at higher levels was also noted by Braby *et al.* (2005).

At lower taxonomic levels, recognition of the generic groupings *Parides* + *Euryades*, [*Trogonoptera* +] *Ornithoptera* + *Troides*, and *Atrophaneura* + *Pachliopta* (including *Losaria*) by Braby *et al.* (2005) appears to be well founded, although they were unable to effectively place the seemingly isolated genera *Pharmacophagus* and *Cressida*. Resolution in these cases is best done using morphological characters that, although subject to various interpretations, strongly suggest a sister-group relationship between *Pharmacophagus* and *Pachliopta* in the first case and between *Cressida* and *Losaria* in the other.

An Indo-Australian plus Madagascan pattern of distribution, as shown by subgenera *Pachliopta* and *Pharmacophagus*, also occurs in pitcher plants (*Nepenthes*: Nepenthaceae) (Heywood 1978) and the fruit fly genus *Dacus* Fabricius (Diptera: Tephritidae), where the largely Indo-Australian subgenus *Neodacus* Perkins is represented in Madagascar by the relatively primitive *xanthaspis* group (Hancock and Drew 2006, White 2006). Furthermore, the largely Indo-Australian butterfly genus *Euploea* Fabricius (Nymphalidae) [and which, like *Pachliopta hector*, is known to be migratory] is represented in the Malagasy region by apparently unrelated endemic species in the Mascarenes and Seychelles, but not in Africa or Madagascar (Holloway and Nielsen 1999). Under the above classification, there is no need to invoke an ancient (pre break-up Gondwana) origin for *P. antenor*, which appears to have differentiated much more recently. Its only confirmed food plant, *Aristolochia acuminata* (= *A. indica*; = *A. tagala*) [also utilised by *P. hector*, *P. polydorus* and *P. aristolochiae* (Fabricius)], is widespread throughout the Indo-Australian region (Sands 2002) and is the only *Aristolochia* species known from Madagascar (Parsons 1996c). *Ar. acuminata* is also likely to be a relatively recent arrival from India and there is no evidence that a suitable host existed in Madagascar [or in Africa] prior to its arrival.

The association of *Cressida* with *Losaria* suggests it is not the Gondwanan relict previously believed but a relatively recent arrival to Australia from a Southeast Asian, *Losaria*-like ancestor. As in the case of *Pharmacophagus*, its dispersal as a small founder population into a new environment might have accentuated its genetic differentiation. In both cases, the modified pupa is likely to reflect a need for crypsis rather than an ancestral state. The various specialisations seen in *Euryades* suggest that it, too, is of relatively recent derivation. Sphragis development in *Cressida*, *Euryades* and *Losaria palu* appears to reflect their dispersal into open habitats, as has been demonstrated in the nymphalid genus *Acraea* Fabricius (Orr 1988).

Phylogenetic relationships of the genera and subgenera, as proposed here, are shown in Fig. 1.

Biogeography

Based on the above morphological evidence, the following biogeographical scenario for the subtribe Troidina is proposed. [For dating see Braby *et al.* 2005 and references therein]. During the continental drifting phase following the break-up of Gondwana, the three main lineages within the subtribe Troidina (Fig. 1) appear to have been confined to the Southeast Asian (or Australian), South American and Greater Indian plates respectively. Assuming Africa had already separated, this dates the fragmentation of the ancestral population at *ca* 90-80 Mya [84-80 Mya if Madagascar is also excluded]. The present restriction of both *Parides* and *Euryades* to Central and/or South America strongly supports the suggestion that these two genera now represent the western lineage of the original Gondwanan ancestor.

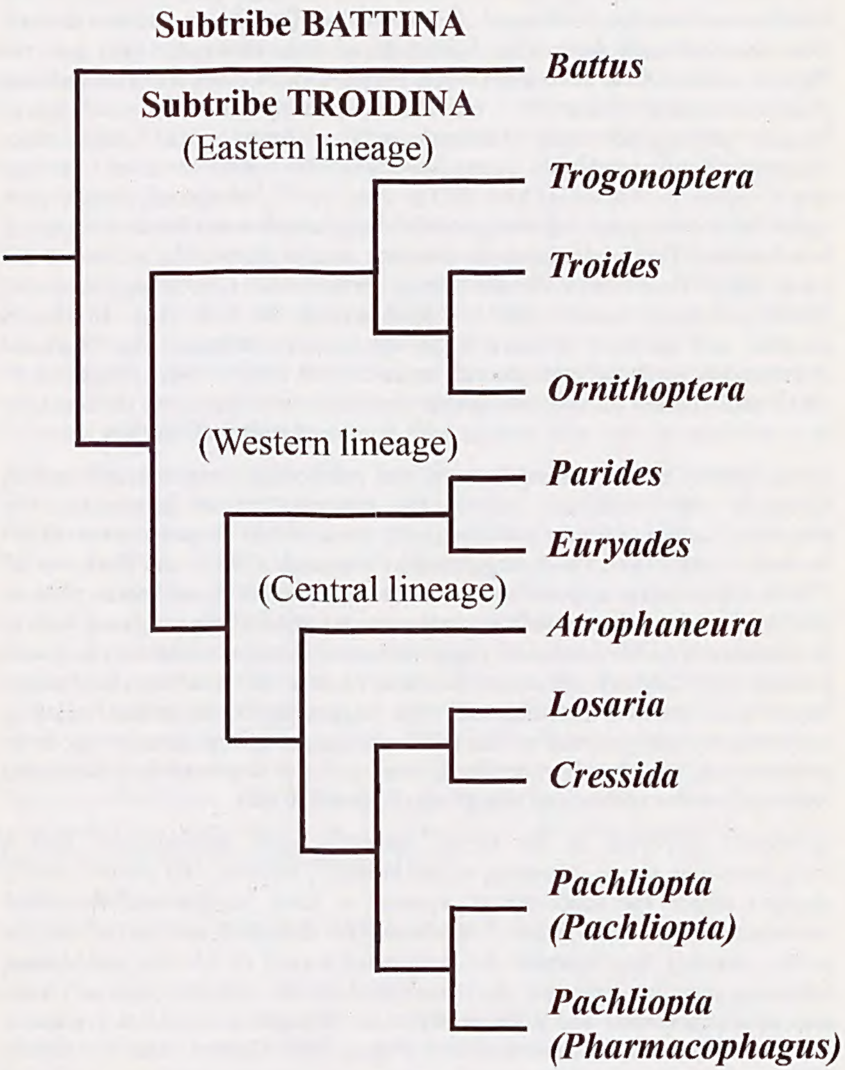

Fig. 1. Suggested phylogenetic relationships of the genera and subgenera of tribe Troidini. See text for discussion of defining character states.

Similarly, the present distributions of *Trogonoptera*, *Ornithoptera* and *Troides* support the suggestion that they represent the eastern lineage of the Gondwanan ancestor. It remains unclear whether the lineage radiated directly from the Southeast Asian (Sundaland) block (see Hancock 1988) into the Papuan subregion via Wallacea [twice, first as *Ornithoptera* via a Sulawesian *Troides* ancestor similar to *T. hypolitus* (Cramer) then, more recently, as *Troides oblongomaculatus* (Goeze)], or (see Braby *et al.* 2005) from Australia into southeast Asia [*Trogonoptera* and *Troides*, leaving *Ornithoptera* in Australia] and, in the case of *T. oblongomaculatus*, back again [with subsequent extinction of the *Trogonoptera* and *Troides* ancestors in Australia]. The former scenario does not require extinctions and seems the more likely. Based on molecular dating, Braby *et al.* (2005) suggested that the *Ornithoptera-Troides* split occurred around 42 ± 8 Mya but this is doubtful and the split is likely to be significantly younger. The Southeast Asian and Australian plates did not make contact until 25 Mya (Braby *et al.* 2005) and whether suitable host plants reached Australia prior to the break-up of Gondwana, or only after contact with Southeast Asia, is uncertain.

Biogeography of the central lineage, the red-bodied *Atrophaneura* and its allies, is more complex. Due to the reassessment of genera such as *Pharmacophagus*, *Losaria* and *Cressida*, the scenario proposed here differs in some details from those suggested by Hancock (1988) and Braby *et al.* (2005). This lineage appears to have been associated with the Indian plate as it broke free from the rest of Gondwana (*ca* 80 Mya), dispersing into Asia as *Atrophaneura* [with increased pupal projections] once contact with it was possible (50-45 Mya). An ability to utilise *Thottea* and *Apama* as host plants might have assisted this dispersal. The suggestion of an Indian origin is supported by the presence of the relatively unspecialised *latreillei* group in eastern Asia, which subsequently appears to have dispersed into Southeast Asia as the more specialised *nox* group (Hancock 1988).

A second dispersal of the Indian ancestor, now differentiated into a *Pachliopta*-like taxon following major climatic, tectonic and environmental changes within the subcontinent, appears to have brought a *Losaria*-like ancestor into Southeast Asia - Sundaland. This dispersal, and that of the *nox* group, possibly accompanied the southward spread of *Thottea* and *Apama* following contact between the Sundaland block and the rest of Asia. Subsequent dispersal and differentiation has brought *Cressida* to Australia, Timor to Tanimbar Is and southern Papua New Guinea, and *Pachliopta* (*Pharmacophagus*) to Madagascar, leaving *Losaria* in southeast Asia and subgenus *Pachliopta* (as *P. hector*) in India. Dispersal to Madagascar possibly took place via the Laccadive-Maldive-Chagos archipelago during a period of lowered sea level. Unlike the condition in *Losaria* and *Cressida*, none of the distinguishing characters of *Pharmacophagus* appear to be distinctive enough to recognise it at generic level; most are homoplasious.

A second major radiation within subgenus *Pachliopta* then appears to have occurred, dispersing again (as the *polydorus* group minus *P. hector*) to Southeast Asia - Sundaland and leaving *P. hector* in India. In these species the wing pattern appears to mimic that of *Losaria*, supporting the suggestion that they radiated first to southeast Asia and from there back to India and Sri Lanka (twice, first as *P. pandiyana* (Moore) + *P. jophon* (Gray), then more recently as *P. aristolochiae*). Subsequent radiations within southeast Asia appear to have resulted in the differentiation of: (1), *P. mariae* (Semper), *P. polyphontes* (Boisduval) and *P. oreon* (Doherty) + *P. liris* (Godart) in the Philippines, Sulawesi and northern Moluccas, and the Lesser Sunda Islands + Timor and neighbouring islands, respectively; (2), the elongate-tailed and largely allopatric *P. schadenbergi* (Semper), *P. leytensis* Muruyama [= *phegeus* (Hopffer)], *P. phlegon* (C. & R. Felder) [= *annae* (C. & R. Felder)] and *P. atropos* (Staudinger) in the Philippines; and (3), *P. polydorus* from the Moluccas to Australia and the Solomon Islands, leaving the widespread *P. aristolochiae* in much of south and southeast Asia, including Sundaland, Sulawesi and the Philippines.

The centre of origin of the tribe Troidini remains unresolved. Braby *et al.* (2005) objected to the suggestion of a North American origin (Hancock 1983) on the grounds that it 'does not explain the absence of the Troidini in Europe and Africa'. However, such absence might merely reflect a lack of suitable host plants or habitat, either now or in the past, or the tribe's failure to disperse there. Within the Troidina the red abdominal hairs, shape of the juxta and loss of the appendix bursae suggest that the *Atrophaneura* group is more closely related to *Parides* + *Euryades* than to the *Troides* group and that the latter is the most primitive. If so, then *Battus* (subtribe Battina) likely is of South American origin, with subtribe Troidina evolving in eastern Gondwana and subsequently dispersing back to South America as the ancestor of *Parides* + *Euryades*. Any original North American ancestor, if such existed, presumably become extinct due to subsequent climatic changes (ice ages) and/or competition from reinvading *Battus*.

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